For the last $\approx 10$ yr, the Gypsy Moth Life Stage (GLS) model has been used by pest managers to predict when important events in the gypsy moth, *Lymantria dispar* L., life cycle will occur (e.g., peak second larval instar population and male moth flight). Although the GLS model has been shown to outperform other gypsy moth phenology models, its predictions have not always been as accurate as desired. Differences between predicted and observed egg hatch phenology prompted a re-examination of the original experimental data that were used in the construction of the egg hatch submodels of the original GLS model, and a data processing error was discovered to have truncated the postdiapause experimental data. Analysis of the complete data set confirmed that developmental rates in the postdiapause phase were age and temperature dependent but that the developmental response to temperature is distinctly nonlinear at postdiapause initiation, in contrast to the indeterminate response previously reported. By incorporating the new estimates of developmental rate patterns and parameters into the GLS model, errors in the GLS-simulated egg hatch period were reduced by 33–71% and error in date of 50% cumulative egg hatch by 25–100%.

**KEY WORDS** age-dependent developmental rate, phenology, temperature, egg phenology

The gypsy moth (*Lymantria dispar* L.) was accidentally released in Medford, MA, in 1868 or 1869 (Liebhold et al. 1989) and has since spread south, north, and west. Defoliating populations are established from North Carolina to New Brunswick and west to Wisconsin. Isolated populations have been detected in other areas such as Missouri, Utah, Oregon, Washington, and British Columbia. For the last several decades, management activities have involved detection and attempted eradication of isolated populations and population monitoring and suppression of established populations. For all of these activities, a prediction of when certain life cycle events (e.g., peak second instar population and male moth flight) will occur is important. During the last $\approx 10$ yr, the Gypsy Moth Life Stage (GLS) model (Gray 2004) has been used to make these predictions in British Columbia (Régnière and Nealis 2002), New Brunswick, Utah (Logan et al. 2006), New Zealand (Pitt et al. 2007), and the 10 American states in the “Slow the Spread” project (Leonard 2007, Roberts and Ziegler 2007).

The GLS model is a composite, multigenerational phenology model (Gray 2004); its acronym also designates the authors of the stage-specific submodels from which it is constructed: Gray et al. (1991, 1995, 2001) for the three distinct phases of the egg stage; Logan et al. (1991) for the early larval stages; and Sheehan (1992) for the late larval to adult stages. The GLS model has perhaps two features unique in the field of insect phenology models. It uses an age-dependent developmental rate function within the postdiapause phase, and it models diapause development as an interaction between a hypothetical temperature-activated agent that inhibits development and the temperature-dependent depletion of the agent. This diapause submodel mimics the manner in which exposure to low temperature facilitates termination of the diapause phase (cold sensibilization *sensu* Zaslavski 1988). Diapause termination is a critical event, particularly in locations where diapause development is slow because of the absence of low winter temperatures, in the ability of a gypsy moth population to maintain the seasonal development that is necessary for population establishment and persistence (Gray 2004).

Field observations of gypsy moth phenology usually involve milestones such as “first egg hatch” or “first pheromone trap capture of a male moth.” Rarely are the observations made frequently enough to construct a complete larval, or male moth, emergence curve of the population. When field observations are frequent enough on a representative sample of egg masses to construct an emergence curve, the observations are rarely accompanied by the daily temperature records, starting at the time of egg oviposition, that are needed to generate a comparable GLS prediction. In the cases where there are frequent field observations that encompass the hatch of the entire egg mass population
and a usable temperature record exists, a comparison of GLS predictions and field emergence has shown that predictions have not always been as accurate as desired. The egg hatch submodels of GLS strongly outperformed the egg hatch submodels of Johnson et al. (1983), Lyons and Lysyk (1989), Nealis et al. (1999), and Sawyer et al. (1993) compared with observed egg hatch in Victoria, British Columbia, Canada (Régnière and Nealis 2002). Nonetheless, GLS predicted 50% cumulative egg hatch 6 d earlier than observed; and the predicted egg hatch period (5th to 95th percentile) was 9 d longer than observed. Similarly, in an unpublished examination of GLS performance, the prediction of 50% cumulative egg hatch was 3 d earlier than observed and the predicted hatch period was 12 d longer than observed in Shenandoah National Park, VA (unpublished data); conversely, the GLS prediction of 50% cumulative egg hatch was 4 d later than observed and the predicted hatch period was 7 d longer than observed in Princess Park, New Brunswick, Canada.

These differences between predicted and observed egg hatch phenology prompted a re-examination of the original experimental data that were used in the construction of the egg hatch submodels of the original GLS model. This paper reports that a data processing error incorrectly identified day 0 of the time-variant postdiapause developmental rate experiment (experiment 2 in Gray et al. 1995) as 2 d later than actual. This single error resulted simultaneously in (1) the inadvertent deletion of the observed egg hatch from five treatments associated with the true day 0; (2) assignment of an incorrect value to “time,” the independent variable in the time-dependent estimates of developmental rates; and (3) the incorrect calculation of elapsed times between postdiapause initiation (day 0) and observations of egg hatch. In this paper, I present the results of an analysis of the full dataset and the corrected parameter values estimated from the full dataset and describe the changes that the corrected postdiapause submodel parameters produced in GLS predictions.

Materials and Methods

**Gypsy Moth Eggs.** Newly laid gypsy moth eggs were obtained from a colony of the New Jersey Standard Strain maintained by the U.S. Forest Service, Northern Research Station (Hamden, CT). Egg masses were exposed to 25°C and a 16:8 (light:dark) photoperiod for 42 d and a 5°C, 16:8 photoperiod for 96 d. This has been shown to be sufficient to initiate (Gray et al. 1991) and complete (Gray et al. 1995: experiment 1) the diapause process. Egg masses were, therefore, just initiating the postdiapause process in the experiments described below.

**Time-variant Developmental Rates in Postdiapause.** A basic assumption in developmental rate experiments has been that the developmental response to a given temperature is constant throughout the life stage (or phase) being examined—the developmental rate at temperature T is the inverse of the time required, at temperature T, to complete the life stage (or phase). Observations of increasing respiration rate in postdiapausing gypsy moth eggs (Gray et al. 1995) suggested that developmental rate at a constant temperature may increase during the postdiapause phase.

Ten egg masses that had just entered postdiapause (t = 0) were each divided between 21 variable-temperature treatments and one constant-temperature (15°C) treatment: ≈25 eggs from each egg mass were assigned to each variable-temperature treatment; the remaining eggs from each egg mass (~300) were assigned to the constant-temperature treatment. All eggs were placed in a 15°C photoperiod environmental chamber on day 0. To test the assumption of a time-invariant response to temperature during postdiapause, eggs within a treatment were transferred on day t from 15°C to an experimental temperature T for 2–10 d and then returned to 15°C. Eggs were exposed to their experimental temperature (T = 5, 10, 20, or 25°C) on days 0, 2, 4, 6, or 8 (4 temperatures × 5 days = 20 treatments). One sample of eggs was exposed to 30°C on day 0 for inclusion in the estimation of R_T(0) (see below). All environmental chambers used a 16:8 (light-dark) photoperiod. Egg hatch was recorded daily. The time-dependent developmental rate response to an exposure to temperature T on day t was estimated for each egg mass i as

\[ R_T(t) = \frac{1 - \frac{t_{15}}{t_T}}{t_{15}}, \]

where \( t_{15} \) is the median time (d) that eggs in the ith egg mass spent at 15°C, \( t_{15} \) is the median time to hatch for the eggs in the ith egg mass in the 15°C constant-temperature treatment, and \( t_T \) is the duration spent at experimental temperature T. The median developmental rate, \( R_T(t) \), was estimated from the 10 egg mass-specific estimates \( R_T(t) \) for each T and t. More eggs from each egg mass were assigned to the constant-temperature treatment than to the variable-temperature treatments because the 21 estimates of \( R_T(t) \) from each egg mass all depend on the one estimate of \( t_{15} \) from the same egg mass. Therefore, it was deemed important to maximize the accuracy of the estimates of \( t_{15} \) for each egg mass.

An analysis of covariance (ANOVA; PROC GLM, SAS Institute 1989) tested the significance of T, t, and their interaction (T × t) on median developmental rate \( R_T(t) \). The effect of T was subsequently removed by dividing each \( R_T(t) \) by the maximum \( R_T \) of the same temperature to create relative developmental rates, \( R_T(t)/\max R_T \). ANOVA tested the significance of T, t, and T × t on \( R_T(t)/\max R_T \) and determined that developmental rate in postdiapause was time variant (see Results). An *Age-dependent Model of Postdiapause Developmental Rates.* The examination of the full dataset (see Results) indicated that developmental rates increased with time in an exponential manner,

\[ R_T(t) = R_T(0) \exp(a_T t), \]
postdiapause, and estimates of $T$

Median developmental rates, from the 10 egg masses, temperature equation 3 for independent function of physiological age by solving where $RT$

Developmental rate at a low temperature at time $C$ is partly is a function of time in a temperature-varying environment. There-

Fig. 1. Time is a nonuniform unit if developmental rate is a function of time in a temperature-varying environment. Developmental rate at a low temperature at time $C$ is partly determined by the value of $C$. If temperature changes to a high temperature, developmental rate should be determined using the value of time $B$.

where $R_F(t)$ is the developmental rate at constant temperature $T$ at time $t$, with $t = 0$ being the onset of postdiapause, and $a_T$ describes the amount of change in the developmental rate per unit time at $T$. Time is an uncertain variable in a model with time-varying and temperature-dependent developmental rates in a changing temperature environment (Fig. 1). Therefore, a description of postdiapause developmental rate as a function of temperature and physiological age was sought. Physiological age is the integral of the rate function (equation 2). The developmental phase is completed (in this case, eggs complete postdiapause and hatch) when the integral equals 1:

$$A_T(t) = \int_0^t R_F(t) \, dt = \frac{R_F(0)}{a_T} \left[ \exp(a_T t) - 1 \right] = 1.0.$$  \[3\]

Developmental rate can be expressed as a time-independent function of physiological age by solving equation 3 for $t$,

$$t = \frac{1}{a} \ln \left( \frac{a_T A}{R_F(0)} + 1 \right),$$  \[4\]

and substituting the result into equation 2:

$$R_F(A) = R_F(0) + a_T A.$$  \[5\]

Estimation of Functions to describe $R_F(0)$ and $a_T$. Median developmental rates, from the 10 egg masses, at each $T$ (5, 10, 20, 25, and 30°C) at $t = 0$ provided estimates of $R_F(0)$ for each $T$. An exponential function,

$$R_F(0) = \tau \times \exp(\delta T),$$  \[6\]

was used to describe the relationship, and parameter values were estimated by nonlinear regression (PROC NLIN; SAS Institute 1999). The extremely small rates of $R_F(0)$ for $T = 5\text{--}20°C$ could not be detected with the precision of daily observations of egg hatch. Therefore, estimates of $R_F(0)$ for these temperatures were obtained by equation 6 when determining estimates of $a_T$ (below).

In a second experiment, 10--12 egg masses that had just entered postdiapause ($t = 0$) were each divided into five approximately equal samples, and samples were placed in either 10, 15, 20, 25, or 30°C until egg hatch. Egg hatch was recorded daily. A 5°C treatment was not included because gypsy moth eggs do not hatch readily at such low constant temperatures. The median time to hatch for each temperature was determined for each egg mass portion, and the median value was calculated from the 10--12 egg mass--specific values. Estimates of $a_T$ were obtained for $T = 10\text{--}30°C$ by solving equation 3, by iteration, for $a_T$ when $A_T(t) = 1$ (hatch), and where $t$ is the median time to hatch at $T$, and $R_F(0)$ is the median developmental rate at $T$ and $t = 0$.

The relationship between $a$ and $T$ was described by a third-degree polynomial,

$$a_T(T) = \omega + \kappa T + \psi T^2 + \vartheta T^3$$  \[7\]

Modeling Developmental Rate Variability. The developmental times from the 10--12 egg masses used in estimating $a_T$ (above) were also used to describe the temperature-independent population variability in postdiapause developmental rates by the “same-shape” procedure of Wagner et al. (1984). The temperature-independent description of developmental rate variability was derived by dividing the inverse of each developmental time ($t$ of equation 3) by the inverse of the median developmental time of the same temperature and egg mass and grouping these relative rates into classes of width 0.05. A three-parameter Weibull function,

$$F(x) = 1 - \exp \left[ -\left( \frac{x - \gamma}{\beta} \right)^a \right],$$  \[8\]

where $F(x)$ is the cumulative probability of relative developmental rate $x$, and $\alpha$, $\beta$, and $\gamma$ are estimated parameters, was fit to the estimated relative rates by nonlinear regression (PROC NLIN; SAS Institute 1999).

Assessing GLS Predictions With New Submodel Parameters. Three sites were selected to compare GLS predictions made with the postdiapause submodel parameters from Gray et al. (1995) with predictions made with the submodel parameters presented here. Sites were selected on the basis of the availability of precise and frequent observations of egg hatch of the entire population, the availability of nearby daily temperature records (daily minimums and maximums) for the entire egg stage, and their intersite differences in climatic regimens.

The Victoria, British Columbia, Canada, site is located at 48.4672° N, 123.4350° W, 30-m elevation, and lies within the temperate/dry summer/warm summer (Csb) climate zone of the Köppen-Geiger climate
Results

Time-invariant Developmental Rates in Postdiapause. A total of 8,794 eggs hatched in the experiment that estimated \( R_T(t) \) (equation 1) and tested for time-variant developmental rates in postdiapause. Mean egg hatch from the variable-temperature treatments (210 combinations of temperature \( \times \) time \( \times \) egg mass portion) was 26.6 (SD = 11.9). Mean egg hatch from the 10 egg mass portions in the 15°C constant-temperature treatment was 323.0 (SD = 157.1).

A visual examination of the developmental response over time (Fig. 2) very clearly indicated that developmental rate was time variant. Developmental rates increased over time at all temperatures tested. The ANCOVA indicated that \( R_T \) was significantly affected by \( t \) (\( F = 36.19; \text{df} = 11.2; P < 0.0001 \)) and the \( t \times T \) interaction (\( F = 3.56; \text{df} = 3.12; P = 0.047 \); Fig. 2). After removing the effect of \( T \) by calculating relative developmental rates \( [R_T(t)/\max R_T] \), the ANCOVA indicated that there was no effect of \( t \times T \) on relative developmental rate, and only \( t \) had a significant effect (\( F = 51.93; \text{df} = 1.12; P < 0.0001 \)). These results indicate that the relative change in developmental rate with increasing age is the same, regardless of the temperature to which eggs are previously, or subsequently, exposed. The relationship between relative developmental rate and temperature was well described (\( R^2 = 0.91 \)) by the exponential model (equation 2; Fig. 3).

Estimation of Functions to Describe \( R_T(0) \) and \( a_T \). Total egg hatch was 1,579 eggs from the variable-temperature treatments of day 0 (postdiapause initiation) that were used to estimate \( R_T(0) \) (equation 6). Mean egg hatch from the 50 combinations of temperature \( \times \) egg mass portion was 31.6 (SD = 12.5). The median developmental rates at postdiapause initiation were 0.00607 and 0.04112/d at 25 and 30°C, respectively. Nonzero rates could not be detected at 5, 10, or 20°C using the precision of daily observations of egg hatch. The relationship between initial developmental rate in postdiapause and temperature was very well characterized by an average temperature of 10–22°C in the warmest month and 0–15°C in the coldest month, and >4 mo with average temperature >10°C.

Egg hatch was monitored daily (with one exception) in 1999, and on-site daily maximum and minimum temperatures were recorded during the entire egg stage (Nealis et al. 1999).

The Gooney Run, VA, site is located at 38.8426° N, 78.475° W, 603-m elevation, and lies within the temperate/without dry season/hot summer (Cfa) climate zone (Peel et al. 2007). This zone is characterized by an average temperature of 10–22°C in the warmest month and 0–18°C in the coldest month. Egg hatch was monitored thrice weekly in 2001, and daily maximum and minimum temperatures were estimated using the temperature generator of BioSIM (Régnière and Bolstad 1994) and the daily records from the Fredericton field station of the Canadian Food Inspection Agency (45.9258° N, 66.6064° W, 19-m elevation).

Predictions of egg hatch from GLS with the submodel parameters estimated from the analysis reported here (hereafter called GLS 2008) were compared with GLS predictions with the previously reported submodel parameters (hereafter called GLS 2004) and to recorded observations of egg hatch using the date of 50% cumulative egg hatch and the duration of the egg hatch period (5–95% cumulative hatch).

![Fig. 2. The relationship between median postdiapause developmental rate \( [R_T(t)/\max R_T] \) and time for four temperatures.](https://academic.oup.com/ee/article/38/1/18/488035/388035)

![Fig. 3. The relationship between median relative developmental rate \( [R_T(t)/\max R_T] \) and time for four temperatures.](https://academic.oup.com/ee/article/38/1/18/488035/388035)
described ($R^2 = 0.99$) by the exponential model (equation 6; Fig. 4). The strong evidence (above) that developmental rate increases exponentially over time (equation 2; Fig. 3) and that eggs hatch after spending the entire phase at temperatures as low as 10°C (equation 2; Fig. 3) and that eggs hatch after spending the entire phase at temperatures as low as 10°C (equation 2; Fig. 3) justifies the use of the exponential model (equation 6) to describe initial developmental rate instead of a linear model that produces values of $R_F(0) = 0.0$ below a temperature threshold of $\approx 23^\circ$C (Fig. 4).

A total of 5,760 eggs hatched from the 12 egg masses in the experiment to estimate $a_T$. Mean egg hatch from the five temperature treatments was 1,152 eggs (SD = 538.9). Median developmental times were 17.46, 9.61, 5.38, 4.22, and 3.03 d for 10, 15, 20, 25, and 30°C, respectively. Estimates of $a_T$ were 0.60133, 0.93489, 1.03908, 0.65646, and 0.27869 for 10, 15, 20, 25, and 30°C, respectively. The cubic function (equation 7) described the relationship between $a_T$ and temperature very well ($R^2 = 0.98$; Fig. 5).

The temperature-independent estimate of population variability in postdiapause developmental rate was very well described ($R^2 = 0.99$) by the Weibull function (equation 8; Fig. 6). Parameter estimates for all functions are presented in Table 1.

Assessing GLS Predictions with New Submodel Parameters. The observed egg hatch period (5-95% cumulative hatch) in Victoria was 30 April to 15 May (16 d); 50% cumulative egg hatch occurred 6 May. GLS 2004 predicted an egg hatch period from 16 April to 10 May (9 d longer than observed) and 50% cumulative egg hatch on 30 April (6 d earlier than observed). GLS 2008 predicted an egg hatch period from 25 April to 16 May (11 d longer than observed) and 50% cumulative egg hatch on 5 May (1 d earlier than observed; Fig. 7).

The observed egg hatch period in Gooney Run was 23 April to 4 May; 50% cumulative egg hatch occurred 30 April. GLS 2004 predicted an egg hatch period from 19 April to 12 May (12 d longer than observed) and 50% cumulative egg hatch on 27 April (3 d earlier than observed). GLS 2008 predicted an egg hatch period from 23 April to 8 May (4 d longer than observed) and 50% cumulative egg hatch on 30 April (0 d different than observed; Fig. 7).

The observed egg hatch period in Princess Park was 14 May to 25 May; 50% cumulative egg hatch occurred 22 May. GLS 2004 predicted an egg hatch period from 17 May to 4 June (7 d longer than observed) and 50% cumulative egg hatch on 26 May (4 d later than observed; Fig. 7). GLS 2008 predicted an egg hatch period from 14 May to 23 May (2 d shorter than observed) and 50% cumulative egg hatch on 19 May (3 d earlier than observed; Fig. 7).

Discussion

In conventional developmental rate experiments, exclusive reliance on measurements of time to complete a life stage is justified by the assumption that developmental response to temperature remains uniform throughout the life stage. This assumption is clearly violated in the case of gypsy moth egg development, as indicated by experiments reported in the literature. Developmental rate is greatest at warm temperatures during early egg ontogeny (Gray et al.
diapause requires some period at low temperatures (Leonard 1968); and egg hatch occurs most quickly under warm temperatures (Johnson et al. 1983). Gray et al. (1991) proposed a three-phase model (prediapause, diapause, and postdiapause), where each phase is distinct and governed by a unique temperature-dependent developmental rate response. In this case, the assumption of a constant developmental response to temperature must hold for each phase. Gray et al. (1995, 2001) subsequently showed that the assumption is violated in the postdiapause and diapause phases, respectively. Submodels of prediapause (Gray et al. 1991) and time-variant models of diapause (Gray et al. 2001) and postdiapause (Gray et al. 1995) were combined with submodels of early-instar development (Logan et al.

Table 1. Parameter estimates for functions describing temperature-dependent initial developmental rates \( R_T(0) \) and developmental rate change \( a_T \) and temperature-independent population variability in developmental rate

<table>
<thead>
<tr>
<th>Function</th>
<th>( \tau )</th>
<th>( \delta )</th>
<th>( \omega )</th>
<th>( \kappa )</th>
<th>( \psi )</th>
<th>( \vartheta )</th>
<th>( \alpha )</th>
<th>( \beta )</th>
<th>( \gamma )</th>
<th>( R^2 )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Initial rate(^a)</td>
<td>3.338182 ( \times 10^{-7} )</td>
<td>0.390727</td>
<td>0.99</td>
<td></td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Rate change(^b)</td>
<td>-1.821620</td>
<td>0.373854</td>
<td>-0.145244286 ( \times 10^{-1} )</td>
<td>1.561466667 ( \times 10^{-4} )</td>
<td>0.98</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Population variability(^c)</td>
<td>2.9140</td>
<td>0.3924</td>
<td>0.6015</td>
<td>0.99</td>
<td></td>
<td></td>
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</table>

\( a_{RT}(0) = \tau \times \exp(\delta T) \)

\( a_T(T) = \omega + \kappa T + \psi T^2 + \vartheta T^3 \)

\( F(x) = 1 - \exp\left[-\frac{(x - \gamma)}{\beta}\right] \)

Fig. 7. Observed egg hatch (●) and simulated egg hatch by GLS 2004 (—) and GLS 2008 (—) in three locations and the minimum and maximum temperatures used in the simulations.
1991) and late instar to adult development (Sheehan 1992) to create GLS 2004 (Gray 2004). However, in their analysis of postdiapause developmental times (Gray et al. 1995), a data processing error inadvertently deleted observations from five treatments and simultaneously incorrectly calculated elapsed time between the initiation of the experiment and observations of egg hatch (i.e., developmental times).

Gray et al. (1995) incorrectly identified day 0 of their experiment 2 (the examination of time-variant developmental rates). Consequently, they used only four time-specific developmental rates, instead of the five that were available, and the independent variable time was incorrectly assigned to each treatment. This resulted in the adoption of an exponential, instead of linear, description of the time-dependent developmental rate function (equation 2) solely on the basis of the convenient simplicity of the ensuing equation 5. The results reported here, using the full dataset and correct variable values, establish that the exponential description is the more appropriate choice given the far superior $R^2$ of the exponential description (0.98) compared with a linear description (0.78; Fig. 3).

The truncation also resulted in inaccurate estimates of developmental rates at time 0 (postdiapause initiation). Consequently, Gray et al. (1995) used a linear function to describe the relationship between developmental rate at postdiapause initiation and temperature, whereas the results from the complete dataset clearly indicate that an exponential relationship is more accurate (Fig. 4). Developmental rates at diapause initiation, as estimated here, are also much lower than those reported earlier (Gray et al. 1995).

The estimates reported here of developmental rate at postdiapause initiation [$R_T(0)$] and median developmental times at a constant temperature produced new estimates of $a_T$ when equation 3 was solved by iteration with $A_T(t) = 1$. The general shape of the relationship between $a_T$ and temperature reported here (Fig. 5) is not different than that reported by Gray et al. (1995), although parameter values are now different (Table 1) and $a_T$ has a markedly higher value at all temperatures than previously reported. Similarly, the general description of population variability in developmental response to temperature is not different than previously reported, but parameter values are now different.

The exponential relationship reported here between developmental rate at postdiapause initiation [$R_T(0)$] and temperature (equation 6) and the cubic relationship between $a_T$ and temperature (equation 7) produces an age- and temperature-dependent developmental rate function that is relatively low at all temperatures (Fig. 8) and virtually insensitive to temperature except at higher (greater than $\approx 20^\circ$C) temperatures (Fig. 4). This differs from the previous results of Gray et al. (1995), where initial developmental rate was more sensitive to temperature throughout the range tested. Nonetheless, the general shape of the age- and temperature-dependent developmental rate curves are not particularly different. The developmental response of eggs that are physiologically young in postdiapause is virtually zero, except at high temperatures. This prevents warm days in late winter or early spring from promoting early egg hatch. After numerous warm days, physiological age will be more advanced, and warm days will have a greater effect on development and hatch.

The exponential relationship reported here between developmental rate at postdiapause initiation and temperature and the new parameter values that produce lower developmental rates at postdiapause initiation [$R_T(0)$] but faster increases in developmental rate as postdiapause progresses ($a_T$) had a pronounced beneficial effect on GLS predictions of egg hatch in the three test sites (Fig. 7). GLS 2008 reduced the error in the simulated egg hatch period by 33% in Victoria (from 9 to 6 d), by 67% in Gooney Run (from 12 to 4 d), and by 71% in Princess Park (from 7 to 2 d). GLS 2008 reduced the error in simulated 50% cumulative egg hatch by 83% in Victoria (from 6 to 1 d), by 100% in Gooney Run (from 3 to 0 d), and by 25% in Princess Park (from 4 to 3 d). It should be noted that these improvements are achieved by retarding the simulated egg hatch in Victoria and by advancing it in Princess Park.

In addition to its use as a pest management tool, GLS 2004 has been used to estimate the risk of establishment of gypsy moth outside its current range (Régnière and Nealis 2002, Gray 2004, Logan et al. 2006, Pitt et al. 2007). Gray (2004) showed that, at high northern latitudes (and presumably southern, as well), the probability of establishment is strongly affected by oviposition date because of the ability of eggs to complete prediapause and enter the cold-hardy diapause phase before temperatures fall below the minimum requirements for prediapause development. Errors in simulated egg hatch phenology will cause errors in simulated oviposition phenology, and therefore, overestimate or underestimate the probability of establishment at the geographic extremes of the potential range of gypsy moth. The significantly improved egg hatch predictions of GLS 2008 will, therefore, also result in improved estimates of the risk of establishment of gypsy moth populations outside its current range.
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